

SPIXIANA	16	1	61-69	München, 30. April 1993	ISSN 0341-8391
----------	----	---	-------	-------------------------	----------------

The arthropod fauna on the bark of deciduous and coniferous trees in a mixed forest of the Itasca State Park, MN, USA.

by Volker Nicolai

Nicolai, V. (1993): The arthropod fauna on the bark of deciduous and coniferous trees in a mixed forest of the Itasca State Park, MN, USA. – *Spixiana* **16/1**: 61-69.

In a mixed stand the fauna living on the bark of ten different North American tree species was investigated: five deciduous and five coniferous. The arthropod fauna living on the bark of trees is very specific for this habitat and does not occur in other habitats of the forest ecosystem. Oribatei, other Acari, Araneae, Chilopoda, Psocoptera, Cicadina, Diptera were found on both deciduous and coniferous bark. Lepidoptera were restricted to the deciduous types. Those deciduous trees having a more structured surface morphology (fissured and scaly bark types) carry more species and more numerous specimens than do the poorly structured (white and smooth) types. Conversely the highly structured bark types of the studied conifers support fewer species in smaller numbers than do the poorly structured types. In total more individuals and more species live on bark of deciduous trees than on bark of conifers. Only few arthropod species are able to live on bark of both types of trees.

Key words: arthropod fauna - trees bark - deciduous and coniferous trees - North America

PD Dr. Volker Nicolai, Philipps-University, Fachbereich Biologie / Zoologie, Postfach 1929 W-3550 Marburg, Germany

Introduction

The structure of trunks and the barks of trees are important factors forming the elements of a specific forest ecosystem. The structural bark form determines the ecological function for bark-living arthropods. Tree barks have been classified into four categories: smooth, white, fissured and scaly (Nicolai 1986). Different bark types have different physiological properties. High insulation capability enables trees to survive such ecological disturbances as forest fires (White 1983, Nicolai 1991). Opened areas resulting from such disturbances leads to successional tree colonisation. Pioneer trees in those areas often have white barks while late successional deciduous trees show more structured barks. These features are to be seen as part of the cyclic mosaic concept of ecosystems (Forcier 1975, Lieberman & Lieberman 1987, Nicolai 1986, 1989 a, b, 1990, Pickett et al. 1989, Pickett 1989, Swaine & Hall 1988, Remmert 1987, 1991, Torquebian 1986). In forest ecosystems the bark-living arthropod communities are adapted to the changes in tree species in space and time (Nicolai 1986, 1989 a).

In central Europe about 100 arthropod species live exclusively on the barks of deciduous trees (Nicolai 1986, 1987 a) the various bark types providing different habitats for them. In this study the differences between arthropod communities living on the barks of coniferous trees were compared and contrasted with those living on the barks of deciduous trees. This analysis is only feasible in an area where both types of species grow naturally together in the same local conditions of soil and climate.

Materials and methods

Study site

The investigations were carried out in the summer of 1989 in the Itasca State Park, Minnesota, U.S.A. (47° 10' N, 95° 15' W). This Park of 3200 ha was formally established in 1891. Two principal types of trees occur there. Predominant are the coniferous tree species *Pinus banksiana* Lamb. *P. resinosa* Ait., *P. strobus* L., *Picea mariana* (Mill.) B.S.P., and *Abies balsamea* (L.) Mill. The deciduous tree species *Acer saccharum* Marsh., *Tilia americana* L., *Quercus macrocarpa* Michx., and *Ulmus americana* L. form the balance.

The bark fauna of both types of trees were studied. A potent abiotic factor affecting tree types and their distribution is the occurrence of fires in this area (Swain 1973). The consequences of these fires account for the vegetative types and variety of age classes that are typical of the forests of the Itasca State Park (Frissell 1973).

Fauna

The bark-living fauna was investigated on the deciduous species *Populus tremuloides* Michx. and *Betula papyrifera* Marsh. (white bark type), on *Tilia americana* and *Fraxinus pennsylvanica* Marsh. (fissured bark type), and on *Acer saccharum* (scaly bark type). Similarly the conifers *Abies balsamea* (smooth bark type), and *Picea mariana*, *Pinus banksiana*, *Pinus resinosa*, and *Pinus strobus* (scaly bark type) were examined. Only adult trees displaying typical bark types were included in the study.

Pooters were used to collect the animals by hand from an area on the trunk 20 cm from the ground to a height of 2.5 m. The whole circumference of the tree was included. The specimens were preserved in 70 % ethanol. Tree species, time of day, weather conditions, girth and position of the tree, and behaviour of the bark fauna was noted. The animals were sorted and counted. Statistical treatment followed that of Mühlenberg (1989). A detailed description and efficiencies of different methods collecting bark dwelling arthropods gives Nicolai (1986).

Results

Table 1 gives a survey of the dominant arthropod groups (>5 % of all collected arthropods on each tree species, N = 11770) living exclusively on the bark of trees in the Itasca State Park. Two different tree species *Populus tremuloides* and *Betula papyrifera* having roughly the same white bark type, showed startling differences in arthropod populations. On the bark of *Populus tremuloides* 35 % of all collected arthropods were Psocoptera, 16 % were Araneae and 14 % were Lepidoptera while the bark of *Betula papyrifera* hosted 37 % Araneae, 22 % Psocoptera and 19 % Oribatei. The comparative proportions of Psocoptera on the scaly-barked *Acer saccharum* was 48.8 % and on the fissured-barked *Tilia americana* 33.4 %. On *T. americana* 23.7 % were Araneae. The fissured-barked *Fraxinus pennsylvanica* showed

Tab. 1 Main arthropod groups (>5% of all collected animals) living on the bark of trees in a North American forest in the Itasca State Park, MN, (%). Pt = *Populus tremuloides*; Bp = *Betula papyrifera*; As = *Acer saccharum*; Ta = *Tilia americana*; Fp = *Fraxinus pennsylvanica*; Ab = *Abies balsamea*; Pm = *Picea mariana*; Pb = *Pinus banksiana*; Pr = *Pinus resinosa*; Ps = *Pinus strobus*. fi = fissured-, sc = scaly-, sm = smooth-, wh = white bark type.

tree species bark type	Pt wh	Bp wh	As sc	Ta fi	Fp fi	Ab sm	Pm sc	Pb sc	Pr sc	Ps sc
Oribatei		19.0	6.4	8.0	8.0	69.4		7.6	19.2	6.4
Acari (Non Oribatei)					11.3					
Araneae	15.9	37.4	9.6	23.1	27.8	21.7	49.4	13.7	42.7	15.7
Chilopoda			9.1	5.1						
Psocoptera	35.1	21.8	48.8	33.4	14.8	5.4	19.6	45.7	17.3	37.0
Cicadina	6.1									
Hymenoptera							6.4			6.4
Formicidae								19.8		6.4
Cecidomyiidae										10.1
Phoridae			5.8							
Lepidoptera	14.3			7.4						
Larvae div.					9.7					
sum (%)	71.4	78.2	79.7	77.6	71.6	96.5	75.4	86.8	79.2	82.0

27.8 % Araneae and 14.8 % Psocoptera proportions. Thus similar bark types do not necessarily yield closely comparative dominant species distribution.

Oribatei, Araneae and Psocoptera were the dominant arthropod groups living exclusively on the investigated coniferous barks. For example, 69.4 % of the collected specimens from the smooth-barked *Abies balsamea* were Oribatei and 21 % Araneae (Table 1). Of the scaly-barked *Picea mariana* and *Pinus resinosa* populations more than 40 % were Araneae, whereas on *Pinus banksiana* and *Pinus strobus* 45.7 % and 37 % respectively were Psocoptera (Table 1).

Oribatei

A total of 19 species of oribatid mites were found (Appendix I). Only one species, in low density, was found on *Populus tremuloides*, *Picea mariana*, and on *Pinus strobus*. Oribatei are highly selective in their choice of deciduous or coniferous habitats. The genera *Platylodes* Berlese, *Liodes* von Heyden, *Scapheremaus* Berlese, *Lucoppia* Berlese, *Neoliodes* Berlese and *Pergalumna* Grandjean were found only on the barks of conifers while the genera *Camisia* von Heyden, *Belba* von Heyden, *Eremaeus* C.L.Koch, *Liacarus* sp.1 Michael, *Oppia* C.L.Koch, *Gymnobates* Banks, *Eporibatula* sp.2 Sellnick, and *Liebstadia* Oudemans were confined to the barks of deciduous trees.

Only five species of Oribatei were found to be living on both deciduous and coniferous barks. They were *Liacarus* sp. 2, *Carabodes* C.L.Koch, *Eporibatula* sp.3, *Scheloribates* sp.1 Berlese and *Oribatella* Banks. Bark surface morphology assumes critical significance in the choice of habitat for various Oribatei species. The more structured barks (fissured and scaly) of the deciduous *Acer saccharum*, *Tilia americana* and *Fraxinus pennsylvanica* attracted more species and greater populations than the smoother white barked *Populus tremuloides* and *Betula papyrifera*. Quite the contrary distributions were found when the coniferous bark populations were evaluated. The smooth-barked *Abies balsamea* supported more species in higher numbers than the more structured barked *Picea mariana*, *Pinus banksiana*, *P. resinosa*, *P. strobus*.

Each tree species had a specific oribatid community which bore similarities to those oribatid communities living on similar bark types. These comparisons were valid for both deciduous and coniferous tree species (Appendix I).

Araneae

Eleven spider species were found on the barks of trees (Appendix I). *Drapetisca alteranda* Chamberlin was found to live on all bark types. It occurs in high numbers per m² on the white-barked *Betula papyrifera* and on the smooth-barked *Abies balsamea*. It was found in lower densities on the other investigated bark types as well (Appendix I). Similar distributions have been described for the European species *Drapetisca socialis* (Sundevall) (Nicolai 1986).

To date 124 spider species have been known to live in the Itasca State Park (Heimer et al. 1984). These authors describe collections of pitfall traps and collections using sweep nets. Nine of the eleven spider species found in the current study were not previously reported as having been identified in the Itasca State Park. These findings suggest that the bark-dwelling fauna is specific to that habitat and does not occupy other parts of the forest.

Psocoptera

Eight species of Psocoptera were identified (Appendix I). The white-barked *Populus tremuloides* carried very few species though many more were identified on the similarly-barked *Betula papyrifera*. *Echmepteryx* sp. Aaron was common to all tree species studied. High numbers of them occurred on the differently textured barks of *Betula papyrifera*, *Acer saccharum* and *Tilia americana* for which species this organism showed a marked, but not exclusive, preference. Another important species of the genus *Metylophorus* Pearman was found to live on the barks of *Acer saccharum* and of *Pinus banksiana*. Generally speaking the Psocoptera in the Itasca State Park show no marked preferences for tree species or bark types.

Diptera

Fourteen taxa of Diptera were distinguished (Appendix I). More taxa were found on richly structured barks (e.g. *Acer saccharum*) than on smooth barks (e.g. *Abies balsamea*). They make use of the bark

environment in a range of their life functions. For example the Empididae species of *Tachypeza* Meigen and the Dolichopodidae species of *Medetera* Fischer use the trunks as hunting areas. The *Neurogona* Rond. (Dolichopodidae) use the trunks as a mating area. For some nocturnal species, e.g. Limoniidae and some Chironomidae, tree trunks provide ideal resting conditions and places of diurnal refuge. These particular species are cryptically coloured (compare Nicolai 1987 b) but others, like the predatory *Tachypeza* are highly conspicuous inhabitants.

Lepidoptera

Lepidoptera were found in significant numbers only on the barks of *Tilia americana*. They were found to be rare on all other investigated trees (Appendix I).

General

Analysis of the numbers of arthropod species and specimens living on the white-barked *Populus tremuloides* and *Betula papyrifera* (Figure 1) shows that approximately only half the number of specimens

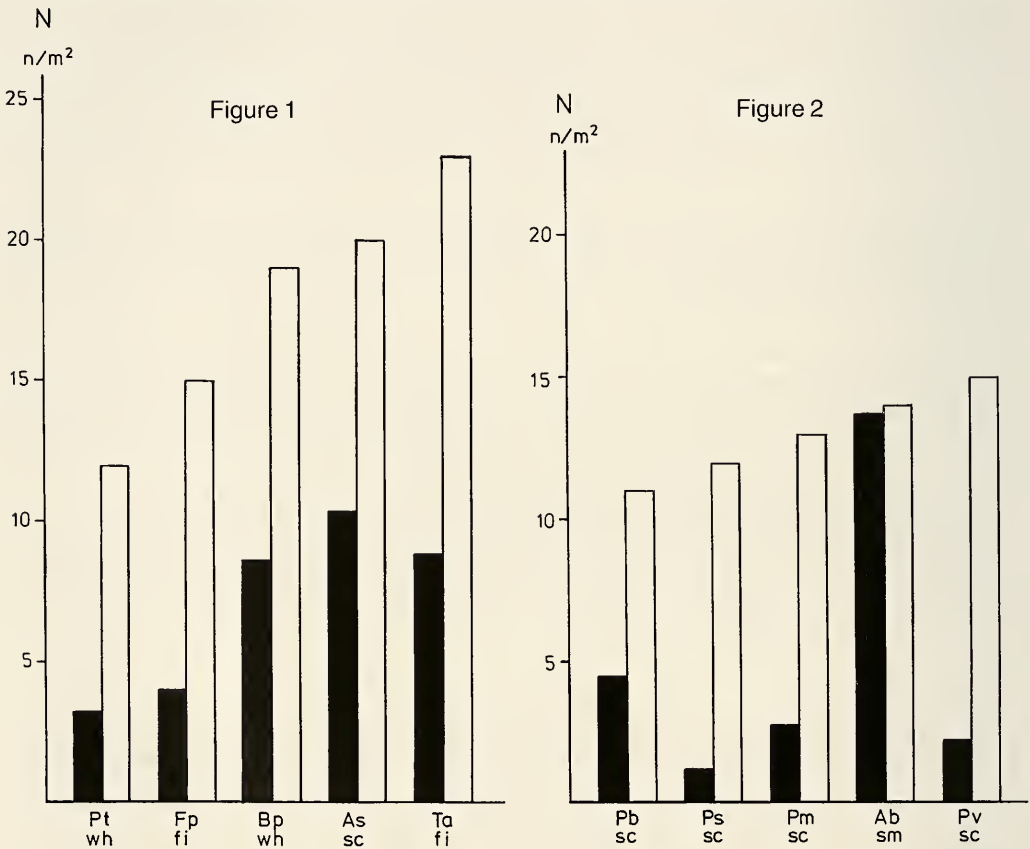


Figure 1: Numbers of arthropod specimens per m² of bark (n/m²) (■) and numbers of arthropod species (N) (□) living on trunks of deciduous tree species in the Itasca State Park, MN. Pt = *Populus tremuloides*; Fp = *Fraxinus pennsylvanica*; Bp = *Betula papyrifera*; As = *Acer saccharum*; Ta = *Tilia americana*. wh = white-, fi = fissured-, sc = scaly bark type.

Figure 2: Numbers of arthropod specimens per m² of bark (n/m²) (■) and numbers of arthropod species (N) (□) living on trunks of coniferous tree species in the Itasca State Park, MN. Pb = *Pinus banksiana*; Ps = *Pinus strobus*; Pm = *Picea mariana*; Ab = *Abies balsamea*; Pr = *Pinus resinosa*. sc = scaly-, sm = smooth bark type.

per m² were found on *Populus tremuloides* compared with those from *Betula papyrifera* which trees also yielded an even smaller proportion of species (Figure 1).

The more structured (fissured and scaly) bark types of *Acer saccharum* and *Tilia americana* bore a greater number of species than their white-barked counterparts (Figure 1). The smooth-barked *Abies balsamea* support many species of Oribatei especially of the genus *Platyliodes* (Appendix I). *Platyliodes* also dominated the specimen count per m² of bark. Of the other arthropod groups found on *Abies balsamea* dominated while the others were rare. The other coniferous species investigated yielded very low densities of arthropods per m² (Figure 2).

Comparisons of species and numbers of specimens per m² found on all tree species demonstrate that higher densities of both elements occur on deciduous than do on coniferous trees (Figure 1, Figure 2) (Mann - Whitney) U-test, $p < 0.05$).

The investigations revealed 60 arthropod taxa living on barks of trees in the Itasca State Park. Almost 80 % of them were found on deciduous trees, about 60 % on coniferous and only 40 % on both.

The variety of species communities living on the barks of deciduous trees differ markedly from those dwelling on conifers. A group of arthropods living only on deciduous barks was identified and a second group that was limited to the barks of coniferous trees. Only few arthropod species are able to live on both kinds of trees, e.g. *Echmepteryx* and *Methylophorus* sp. (Appendix I). *Camisia* sp., *Belba* sp. (Oribatei), *Tachypeza* sp. (Diptera, Empididae) (Appendix I) were restricted to deciduous trees while *Platyliodes* sp. and *Liodes* sp. (Oribatei) are examples of arthropods living only on barks of coniferous trees (Appendix I).

Discussion

Openings are natural components of forest ecosystems (Lang and Knight 1983, Rimmert 1985, 1987, Schrempf 1986). They may be created as a consequence of a variety of disturbances. The degree of diversity of the resultant forest ecosystem is related to the severity and frequency of the impact of the causative agency (Connell & Slatyer 1977, Connell 1978, Denslow 1980, Jacobs 1988, Whitmore 1989). Natural agencies responsible for clearance causation may be fires (Stewart 1986, Uhl & Jordan 1984, Uhl et al. 1988, Zackrisson 1977), wind (Brewer & Merritt 1978), animals (Basey et al. 1988, Smith & Goodman 1987), phytophagy (Whitney 1984), disease (Menges & Loucks 1984), or even volcanic eruptions (Spies & Franklin 1989).

Forest openings are first colonized by so-called pioneer species of trees which have a white bark type (e.g. *Betula pendula* in central Europe; *Populus tremuloides* and *Betula papyrifera* in North America). Their reflective powers protect the trees from overheating by global radiation (Nicolai 1986, 1987 a, 1989 a, b, 1990). Few arthropod species live on these white barks.

Other deciduous trees may establish themselves as successional species in the forest openings. They have more structured barks some of which have good thermal insulation properties which confers an ability to survive disturbances like forest fires. Trees so protected are able to carry larger populations of arthropod species and specimens. As natural forests are composed of trees with different bark types the advent of richly structured-barked tree colonisation broadens the opening's developing fauna.

The regeneration of some North American pine species (*Pinus banksiana*, *P. resinosa*, *P. strobus*) is dependent on fire, and the present day mosaic forest in the Itasca State Park is a result of different historic fires in the specific areas of the park (Frissel 1973). Maissurow (1941) noted that 95 % of the virgin forests in Northern Wisconsin had been burned within the last five centuries. These reports emphasise the importance of fire as a natural ecological factor in North American forests. Not only do trees have to adapt to this factor of disturbance but so do all the other forest plants and animals too.

The acceptance of fire as a naturally-occurring ecological factor establishes the protective function of bark in enabling trees to withstand fire hazards. The bark of *Pinus strobus* was found to have the highest degree of thermal insulation (Nicolai 1990). That of *Pinus resinosa* displays limited ability to resist fire but *Abies balsamea* and *Picea mariana* are so feebly protected that they cannot survive forest fires. Apart from this defensive property tree barks have other ecological functions. They form the habitat of choice for a range of arthropods some of which dwell exclusively there. The smooth-barked conifer *Abies balsamea* shelters an arthropod community almost wholly consisting of the oribatid mite

species *Platylodes* sp.. All other investigated conifers had scaly bark but they, somewhat surprisingly, supported fewer species and specimens of arthropods per m² than the smooth-barked variety (Figure 2).

Southwood (1961) advanced the hypothesis that more abundant trees have high insect populations. In Russia, with its enormous tree count, more insects live on the indigenous conifers than do on the introduced conifers of Great Britain. In Russia too relatively more insects live on coniferous trees than do on the deciduous varieties. The precise opposite of this distribution is the case in Great Britain.

The Itasca State Park is part of a North American area where coniferous and deciduous trees form mixed forests. The phenomenon of naturally-occurring mixed woodland is not found in Europe where natural forests are either coniferous or deciduous. It was in the latter that arthropod fauna distribution studies on barks were carried out (Nicolai 1986). On the more structured barks of central European deciduous woodlands more arthropod species and specimens were found than on poorly structured barks (Nicolai 1986). In the mixed forest of the Itasca State Park the principal difference between arthropod communities living on the barks of coniferous and deciduous trees is that relatively low numbers of species (N/m²) and specimens (n/m²) occur on the highly-structured barks of *Pinus strobus*, *P. resinosa* and *P. banksiana* whereas higher numbers of both counts live on the smooth-barked *Abies balsamea*.

Quite the opposite distribution occurs in European forest ecosystems. There the smooth-barked deciduous trees (e.g. *Fagus sylvatica* L.) bear relatively low numbers of arthropod species while highly-structured barks of the same leaf types, e.g. *Quercus robur* L., have much denser and richer populations (Nicolai 1986). These distributions on barks of central European trees are confirmed by the Itasca State Park findings on deciduous trees (Figure 1).

The studies have thus shown that deciduous tree arthropod fauna living on the barks of pioneer species (e.g. *Populus tremuloides* in North America and *Betula pendula* in central Europe) is sparse. Diversity of bark-living fauna increases on successional deciduous trees with differentiated barks. The reverse was found to be the case for the arthropod fauna living on coniferous trees.

Acknowledgements

For helpful discussions, comments and support during the study I thank Prof. Dr. H. Remmert (University of Marburg, Federal Republic of Germany) very much. I wish to thank Prof. Dr. D. F. Parmelee (James Ford Bell Museum of Natural History, University of Minnesota) for all his help and his interest in this work. Thanks are due to Prof. Dr. D. B. Siniff (Director, Itasca Biology Program, University of Minnesota) for providing of working facilities. I wish to thank J. Ross (Resident Biologist, Itasca State Park, University of Minnesota) for introductions in the forests in the Itasca State Park. For help with determinations of spiders thanks are due to Dr. B. Cutler (Director, Electron Microscopy Laboratory, University of Kansas), Dr. C. D. Dondale (Biosystematics Research Institute, Ottawa, Canada), and J. Wunderlich (Straubenhardt, Federal Republic of Germany). Thanks are also extended to R. Ziegenbein for her corrections of the English text. I wish to thank Derek Bielby (North Yorkshire, U.K.) for his valuable comments on the manuscript. The studies have been rendered possible by the tolerance of my family.

References

- Basey, J. M., Jenkins, S. H. & P. E. Busher. 1988. Optimal central-place foraging by beavers: tree-size selection in relation to defensive chemicals of quaking aspen. - *Oecologia* **76**: 278-282
- Brewer, R. & P. G. Merritt. 1978. Wind throw and tree replacement in a climax beech-maple forest. - *Oikos* **30**: 149-152
- Connell, J. H. & R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. - *Am. Nat.* **111**: 1119-1144
- Connell, J. H. .1978. Diversity in tropical rain forests and coral reefs. - *Science* **199**: 1302-1310
- Denslow, J. S. 1980. Patterns of plant species diversity during succession under different disturbance regimes. - *Oecologia* **46**: 18-21
- Forcier, L. K. .1975. Reproductive strategies and the co-occurrence of climax tree species. - *Science* **189**: 808-810
- Frissell, S. S. 1973. The importance of fire as a natural ecological factor in Itasca State Park, Minnesota. - *Quaternary Res.* **3**: 397-407
- Heimer, S., Nentwig, W. & B. Cutler. 1984. The spider fauna of the Itasca State Park (Minnesota, U.S.A.). - *Faun. Abh. Staatl. Museum Tierk. Dresden* **11** (6): 119-124
- Jacobs, M. 1988. *The Tropical Rain Forest*. - Springer, Berlin, Heidelberg, New York, 295pp.

- Lang, G. E. & D. H. Knight. 1983. Tree growth, mortality recruitment, and canopy gap formation during a 10-year period in a tropical moist forest. - *Ecology* **64**: 1075-1080
- Lieberman, D. & M. Lieberman. 1987. Forest tree growth and dynamics at La Selva, Costa Rica (1969-1982). - *J. Trop. Ecol.* **3**: 347-358
- Maissurrow, D. K. 1941. The role of fire in the perpetuation of virgin forests of northern Wisconsin. - *J. Forestry* **39**: 201-207
- Menges, E. S & O. L. Loucks. 1984. Modeling a disease-caused patch disturbance: oak wilt in the midwestern United States. - *Ecology* **65**: 487-498
- Mühlenberg, M. 1989. Freilandökologie. 2.ed. - Ouelle&Meyer, 430pp.
- Nicolai, V. 1986. The bark of trees: thermal properties, microclimate and fauna. - *Oecologia* **69**: 148-160
- 1987 a. Trees have also protection against the sun's rays. - Reports of the DFG 2/86 german research 9-11
- 1987 b. Anpassungen rindenbesiedelnder Arthropoden an Borkestruktur und Feinddruck. - Spixiana (München) **10** (2): 139-145
- 1989 a. Thermal properties and fauna on the bark of trees in two different African ecosystems. - *Oecologia* **80**: 421-430
- 1989 b. Mikroklima und Fauna mitteleuropäischer und afrikanischer Baumrinden. - *Verh. Ges. Ökol.* **17**: 417-424
- 1990. The ecological roles of barks of trees during forest dynamics and their implication for practical forestry. - *Zool. Jb. Syst.*, in press
- 1991. Reactions of the fauna on the bark of trees to the frequency of fires in a North American savanna. - *Oecologia* **88**: 132-137
- Pickett, S. T. A. 1989. Space-for-time substitution as an alternative to long-term studies. In: Likens GE (ed): Long-term studies in ecology: approaches and alternatives. pp. 110-135. - Springer, Berlin, Heidelberg, New York
- Kolasa, J., Armesto, J. J. & S. L. Colins. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. - *Oikos* **54**: 129-136
- Remmert, H. 1985. Was geschieht im Klimax-Stadium? - *Naturwiss.* - **72**: 505-512
- 1987. Sukzessionen im Klimax-System. - *Verh. Ges. Ökol.* **16**: 27-34.
- 1991. (ed). The mosaic-cycle-concept of ecosystems. - *Ecol. Studies* Vol. **85**
- Schrenpf, W. 1986. Waldbauliche Untersuchungen im Fichten-Tannen-Buchen-Urwald Rothwald und in Urwald-Folgebeständen. - Ph.D. thesis, Univ of Wien, 124pp.
- Smith, T. M. & P. S. Goodman. 1987. Successional dynamics in an *Acacia nilotica* - *Euclea divinorum* savannah in Southern Africa. - *J. Ecol.* **75**: 603-610
- Southwood, T. R. E. 1961. The number of species of insect associated with various trees. - *J. Animal. Ecol.* **30**: 1-8
- Spies, T. A. & J. F. Franklin. 1989. Gap characteristics and vegetation response in coniferous forests of the pacific northwest. - *Ecology* **70**: 543-545
- Stewart, G. H. 1986. Population dynamics of a mountane conifer forest, western cascade range, Oregon, U.S.A. - *Ecology* **67**: 534-544
- Swain, A. M. 1973. A history of fire and vegetation in northeastern Minnesota as recorded in Lake sediments. - *Quaternary Res.* **3**: 383-396
- Swaine, M. D. & J. B. Hall. 1988. The mosaic theory of forest regeneration and the determination of forest composition in Ghana. - *J. Trop. Ecol.* **4**: 253-269
- Torquebian, E. F. 1986. Mosaic patterns in dipterocarp rain forest in Indonesia, and its implication for practical forestry. - *J. Trop. Ecol.* **2**: 301-325
- Uhl, C. & C. F. Jordan. 1984. Succession and nutrient dynamics following forest cutting and burning in Amazonia. - *Ecology* **65**: 1476-1490
- Kauffman, J. B. & D. L. Cummings. 1988. Fire in the Venezuelan Amazon 2: environmental conditions necessary for forest fires in the evergreen rainforest of Venezuela. - *Oikos* **53**: 176-184
- Whitemore, T. L. 1989. Canopy gaps and the two major groups of forest trees. - *Ecology* **70**: 536-538
- Whitney, G. G. 1984. Fifty years of change in the arboreal vegetation of Heart's content, an old-growth Hemlock-White Pine-Northern hardwood stand. - *Ecology* **65**: 403-408
- Zackrisson, O. 1977. Influence of forest fires on the North Swedish boreal forest. - *Oikos* **29**: 22-32

Appendix I

Appendix I: Arthropods living on the bark of trees in the Itasca State Park, MN (numbers of specimens per m² of bark). Pt = *Populus tremuloides*; Bp = *Betula papyrifera*; As = *Acer saccharum*; Ta = *Tilia americana*; Fp = *Fraxinus pennsylvanica*; Ab = *Abies balsamea*; Pm = *Picea mariana*; Pb = *Pinus banksiana*; Pr = *Pinus resinosa*; Ps = *Pinus strobus*. fi = fissured-, sc = scaly-, sm = smooth-, wh = white bark type.

tree species bark type	Pt wh	Bp wh	As sc	Ta fi	Fp fi	Ab sm	Pm sc	Pb sc	Pr sc	Ps sc
Oribatei										
<i>Canisia</i> sp.			0.055	0.051						
<i>Platylodes</i> sp.						7.648	0.043		0.043	0.038
<i>Belba</i> sp.			0.055	0.051						
<i>Liodes</i> sp.								0.038		
<i>Eremaeus</i> sp.			0.055							
<i>Liacarus</i> sp. 1					0.131					
<i>Liacarus</i> sp. 2					0.065	0.879				
<i>Carabodes</i> sp.			0.055			0.067				
<i>Oppia</i> sp.		0.059								
<i>Scapheremaeus</i> sp.								0.038		
<i>Gymnobates</i> sp.					0.065					
<i>Lucoppia</i> sp.						0.203				
<i>Eporibatula</i> sp.1				0.102						
<i>Eporibatula</i> sp. 2				0.102				0.076	0.043	
<i>Liebstadia</i> sp.	0.049	0.051		0.051						
<i>Scheloriobates</i> sp. 1		0.659	0.165						0.028	
<i>Oribatella</i> sp.			0.055	0.051					0.043	
<i>Neoliodes</i> sp.						0.067				
<i>Pergalumna</i> sp. 1						0.406				
Araneae										
<i>Drapetisca alteranda</i>		0.839		0.306	0.065	2.707	0.175			0.038
<i>Soulgas corticalis</i>		0.119	0.055	0.204			0.043	0.038		
<i>Theridion</i> sp.					0.065					
<i>Pardosa mackenziana</i>		0.059								
Agelinidae		0.059				0.067				
<i>Amaurobius</i> sp.									0.021	
Erigonine sp.										0.019
<i>Coriarachne utahensis</i>		0.059	0.055		0.131		0.264			
<i>C. utahensis x versicolor</i>							0.043			
<i>Eris militaris</i>				0.102		0.067				
<i>Platycryptus undatus</i>									0.021	
juvenile Gen.	0.494	1.619	0.885	1.836	0.852	0.270	0.614	0.575	0.873	0.114
Psocoptera										
<i>Echmepteryx</i> sp.	0.791	1.499	1.106	2.551	0.459	0.541	0.351	0.191	0.327	0.133
<i>Liposcelis</i> sp.		0.179								
<i>Epipsocus</i> sp.									0.021	
<i>Blaste</i> sp.		0.059			0.065					0.019
<i>Metylophorus</i> sp.	0.049	0.059	3.928			0.067	0.087	1.764		
<i>Copostigma</i> sp.					0.065					
<i>Ptycta</i> sp.				0.357						
<i>Myopsocus</i> sp.		0.059					0.087	0.038	0.021	0.152
Diptera										
Chironomidae	0.049		0.33	0.20	0.13					0.05
Ceratopogonidae			0.05	0.10						
Psychodidae	0.049						0.043			
Cecidomyiidae			0.16	0.05	0.06				0.02	0.11

Appendix I continued

tree species bark type	Pt wh	Bp wh	As sc	Ta fi	Fp fi	Ab sm	Pm sc	Pb sc	Pr sc	Ps sc
Sciaridae		0.11			0.06					0.019
Limoniidae			0.05					0.038		
Culicidae		0.05	0.16	0.05	0.06	0.06	0.086			
Phoridae	0.049	0.11	0.60	0.35				0.038	0.02	
Empididae:										
<i>Tachypeza</i> sp.	0.098		0.055							
Dolichopodidae:										
<i>Medetera</i> sp.	0.148						0.043	0.038		
Pallopteridae	0.049									
Muscidae				0.05					0.02	0.019
Chloropidae		0.179								0.019
Chyromyidae			0.055							
Lepidoptera										
Nepticulidae									0,02	
Incurvariidae sp. 1	0.247			0.051						
Tineidae				0.051						
Talaeporiidae larvae				0.051						
Pyralidae sp. 1				0.255						
Pyralidae sp. 2	0.197	0.119	0.055	0.255						
Pyralidae sp. 3						0.067	0.067		0.02	
Noctuidae sp.					0.065					